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Rapid fuel recovery after stand-replacing fire in closed-cone pine forests and implications for short-interval severe reburns

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ABSTRACT

Accelerating disturbance activity under a warming climate increases the potential for multiple disturbances to overlap and produce compound effects that erode ecosystem resilience — the capacity to experience disturbance without transitioning to an alternative state. A key concern is the potential for amplifying or attenuating feedbacks via interactions among successive, linked disturbance events. Following severe wildfires, fuel limitation is a negative feedback that may reduce the likelihood of subsequent fire. However, the duration of, and pre-fire vegetation effects on fuel limitation remain uncertain. To address this knowledge gap, we characterized fuel profiles over a 35-year post-fire chronosequence in California closed-cone pine forests, a system with stand dynamics comparable to stand-replacing fire regimes in other temperate and boreal conifer forests with much longer fire return intervals. We used this system to ask: 1) How do fuel profiles change with time since recent stand-replacing fire? 2) How do trajectories of fuel profiles differ between forests established from different pre-fire vegetation legacies — specifically areas that were forest vs. non-forest pre-fire? We also assessed fuel profiles that supported stand-replacing fire during a large (>90,000 ha) wildfire that burned through our study area shortly after data collection and compared with fuel profiles across the chronosequence. Overall, live and dead surface fuels accumulated quickly, reaching levels comparable to those capable of supporting severe fire after 10–15 years. Canopy fuels peaked at 20 years post-fire but were at levels comparable to those capable of supporting severe fire from 15 years onwards. Pre-fire vegetation legacy drove divergence in post-fire dead surface fuel trajectories, but effects on live surface and canopy fuels were minor. Fuel profiles in California closed-cone pine forests can support subsequent severe fire within 10 years, a fraction of the historical minimum interval between stand-replacing fires (≥30 years) that supports robust post-fire regeneration, but potential for severe fire remains lower for an extended period in areas where pre-fire vegetation was non-forest. Our findings show that the negative feedback of fuel limitation disappears quickly following fire, suggesting that these systems are vulnerable to short-interval severe reburns that could erode forest resilience.

1. Introduction

Climate change is altering terrestrial ecosystems globally through changes to disturbance regimes (Trumbore et al., 2015). Changing disturbance regimes linked to warming climate have been documented for forested ecosystems globally (Millar and Stephenson, 2015; Prichard et al., 2017; Seidl et al., 2014), and changes in frequency, size, and/or severity of disturbances may have abrupt and substantial effects on ecosystem structure and function (Turner, 2010). A key concern underpinning these effects from changing disturbance regimes is the potential for erosion of forest resilience, defined as the capacity of an ecosystem to experience disturbance without transitioning to an alternative state (Holling, 1973).

Changing disturbance regimes may increase the likelihood of synergistic interactions among disturbances. Fire activity in many forested ecosystems between the early 2000s to the early 2020s (Boer et al.,

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2020; Higuera and Abatzoglou, 2020) has been characterized by increases in fire season length (Balch et al., 2017; Jolly et al., 2015), average fire size (Dennison et al., 2014), annual area burned (Abatzoglou et al., 2021; Collins et al., 2022; Littell et al., 2009), fire frequency (Brown and Johnstone, 2012; Fairman et al., 2017; Turner et al., 2019), and proportion area burned with high severity (Collins et al., 2021; Parks and Abatzoglou, 2020). While many ecosystems were historically characterized by high-severity fire regimes, one consequence of increases in fire activity in these ecosystems is that overlapping fires can occur at substantially shorter intervals than the historical fire return interval (i.e., short-interval severe reburns; Donato et al. 2009). When they occur, short-interval severe reburns can erode material legacies (*sensu* Johnstone et al. 2016) — including surviving trees, standing snags and seed source — and may produce compound (*sensu* Paine et al. 1998) or synergistic effects on ecosystems (Harvey et al., 2023). Such compound effects from short-interval severe reburns can manifest as decreased abundance of a formerly dominant tree species (Bowman et al., 2014; Enright et al., 2014; Turner et al., 2019), altered forest structure (Fairman et al., 2017), or conversion from forest to non-forest (Brown and Johnstone, 2012).

A key constraint on compound disturbance occurrence is whether disturbances are linked (*sensu* Simard et al. 2011); that is, whether one disturbance can affect the likelihood or magnitude of a subsequent disturbance. In the case of short-interval severe reburns, the occurrence of one stand-replacing fire may be negatively linked with the occurrence of a severe reburn through negative feedbacks on fuel availability. Fuel limitation immediately following severe fire can reduce the likelihood of subsequent fire (Fontaine et al., 2012; Harvey et al., 2016; Parks et al., 2016, 2015), but the duration of fuel limitation varies with species composition and stand dynamics (Prichard et al., 2017). In forests where fire activity is not fuel-limited and rather is strongly controlled by the occurrence of an ignition (ignition-limited) or antecedent weather conditions (climate-limited; *sensu* Littell et al. 2009), fuel loads were historically of relatively low importance for understanding fire potential (Romme 1982, Moritz et al. 2004). Given a warming climate and increasing anthropogenic ignitions (Balch et al., 2017; Westerling et al., 2011), increases in fire initiation and spread in forests with climate- or ignition-limited fire regimes are highly likely. Previous studies in forests with climate- or ignition-limited high-severity fire regimes suggest that fuels sufficient to carry fire are present within a fraction of the time of the mean fire return interval following wildfire (McNamara et al., 2019b; Nelson et al., 2016, 2017).

Feedback duration and magnitude from prior disturbance (e.g., fuel limitation), likely differ depending on the legacy of pre-disturbance vegetation, with important implications for forest contraction or expansion. The potential for forest contraction following short-interval severe reburns is of particular concern for management of forests dominated by serotinous obligate seeders – species with low ability to survive fire and that regenerate from an on-site canopy seed bank (Lamont et al., 1991). Where reburn frequency outpaces canopy seed bank development, serotinous populations are unlikely to persist (Enright et al., 2015). Conversion from forest to non-forest following short-interval severe reburns has already occurred in some forests dominated by serotinous obligate seeders in both North America (Brown and Johnstone, 2012; Turner et al., 2019) and Australia (Bowman et al., 2014). Alternatively, for serotinous species that reach reproductive maturity at an early age, forests have the potential to expand into non-forest ecosystems following periods characterized by high levels of fire activity (Buma et al., 2013; Johnstone and Chapin, 2003; Krause and Whitlock, 2017; Reilly et al., 2019). Expansion of serotinous tree species into pre-fire grassland or shrub-dominated ecosystems has occurred after single severe fire events (Forrestel et al., 2011; Harvey et al., 2011), suggesting that non-forest to forest conversion represents a separate post-fire pathway possible in systems characterized by a forest and non-forest mosaic. Forests established from different pre-fire vegetation legacies (e.g., forest vs. non-forest pre-fire) are likely to differ with respect to post-fire structural attributes, such as standing snag and downed woody surface fuel abundance (Fig. 1). Differences in how pre-fire vegetation legacy affects severe reburn potential may have important implications for linked disturbance interactions.

In addition to building a better understanding of linked interactions among fires, understanding fuel profile trajectories has strong relevance to fuels management. Fuel reduction treatments are deployed in fire-prone forests to decrease subsequent wildfire intensity and to protect life and infrastructure, but resources and capacity to deploy treatments are limited (Agee and Skinner 2005). Understanding how fuel profiles develop continuously over time and when fuels can support severe fire can provide insights on the efficacy and longevity of treatment application.

The closed-cone pine forests of California, USA, are a model system for understanding the mechanisms of serotinous forest resilience to short-interval severe reburns. These forests are characterized by a stand-replacing fire regime like other serotinous forests in North America (e.g., lodgepole pine [*Pinus contorta*], jack pine [*P. banksiana*]), but stand development occurs more rapidly (Harvey et al., 2011; Vogl, 1973). California closed-cone pines reach reproductive maturity at a younger age and proceed through the stages of stand dynamics more quickly than other serotinous forests in North America (Agne et al., 2022a; Bisbing et al., 2023; Harvey and Holzman, 2014; Keeley et al., 1999). These forests experience stand-replacing fire relatively frequently, with mean fire return intervals on the order of decades (Sugnet, 1985; van de Water and Safford, 2011; Vogl, 1973), compared with centuries for other North American serotinous forests (Gauthier et al., 1996; Romme, 1982). Therefore, empirically characterizing fuel profiles across the inter-fire period is more logistically feasible than in most other serotinous forests in North America. Insights from California closed-cone pine forests may illuminate the mechanisms driving fire regimes and species persistence in forests in which these processes unfold on much longer temporal scales.

To understand the mechanisms underpinning the likelihood of short-interval severe reburns at the stand scale in serotinous conifer forests, we conducted a field study of trends in fuel accumulation over a time since fire (TSF) gradient in California closed-cone pine forests dominated by either bishop pine (*Pinus muricata*) or knobcone pine (*P. attenuata*). We asked: 1) how do fuel profiles, including live and dead surface and canopy fuel loads, change with TSF, and 2) how do trajectories of fuel profiles differ between forests established from different pre-fire vegetation legacies — specifically areas that were forest vs. non-forest pre-fire? We expected trends similar to fuel profile development in other serotinous forests (Nelson et al. 2016, McNamara et al. 2019b) but that the accelerated pace of stand development in California closed-cone pine forests would lead to more rapid fuel accumulation. Specifically, with increasing TSF, we expected live and dead surface fuel loads to increase and plateau after the period of snagfall and canopy closure and the canopy fuel load to increase continuously. Further, because pre-fire forest successional age can affect fuel profiles (Nelson et al., 2016), we expected stands that were forest preceding the last fire to have greater peak live and dead surface, as well as canopy fuel loads compared to stands that were previously non-forest. Finally, we assessed fuel profiles that burned with stand-replacing and non-stand-replacing fire during a large (>90,000 ha) wildfire that burned through our study area shortly after data collection and compared with fuel profiles across the chronosequence. Our study provides key insight for management of forested ecosystems in which short-interval severe reburns can occur and for where fuels management could alter the period of fuel limitation (Agee and Skinner, 2005).

2. Materials and methods

2.1. Study area

The study area is bounded by the coastal mountain ranges and Sierra

Fig. 1. Fuel profiles at various times since fire (TSF) in closed-cone pine forests that were characterized by forest preceding the most recent fire (left column) or non-forest preceding the most recent fire (right column).

Cascade foothills in northern and central California and spans the distributions of bishop and knobcone pine in California where stand-replacing fire has occurred since 1982 (Appendix: Figure A1). The study area encompasses low elevation to lower montane zones (84–1344 m above sea level) and has a Mediterranean climate with hot, dry summers and cool, wet winters. The climate covers a wide range of average winter (January) temperatures (3.3–12.2 °C), average summer (July) temperatures (14.9–26.9 °C), and annual average precipitation (467–1996 mm; 800-m gridded 30 year climate normals from 1981 to 2010 [PRISM Climate Group 2019]). Bishop pine occupies areas that receive less total precipitation (annual average precipitation of 467–1034 mm) than where knobcone pine occurs (785–1996 mm). Further, bishop pine occupies areas that experience lower variation in temperature across seasons, with averages ranging from 8.8 to 12.2 °C in January and 14.9–18.7 °C in July vs. 3.3–9.9 °C in January and 20.7–26.9 °C in July for knobcone pine. Both species experience strong seasonality in precipitation (with at least 94% falling between October and May [PRISM Climate Group 2019]) and a moderating effect of summer fog (Torregrosa et al., 2016; Vogl et al., 1977). Closed-cone pine plant communities are often densely forested but are also represented by low density, open stands that overtop chaparral and co-occur with diverse shrub and herbaceous communities. Although both knobcone and bishop pine can occur as co-dominant with other conifer species such as Douglas-fir (*Pseudotsuga menziesii*) (Finney and Martin, 1989; Vogl et al., 1977), this study focused on monodominant closed-cone pine stands. Common co-occurring shrub species include chamise (*Adenostoma fasciculatum*), toyon (*Heteromeles arbutifolia*), and evergreen huckleberry (*Vaccinium ovatum*) as well as a variety of *Ceanothus* spp. and *Arctostaphylos* spp. Resprouting broadleaf trees, most commonly *Quercus* spp., are also represented on the landscape, and this ecosystem is characterized by a high diversity of herbaceous vegetation, including *Acmispon glaber*, *Lupinus* spp., and *Mimulus* spp.

In stands where closed-cone pines are monodominant, the historical fire regime is generally characterized by stand-replacing fire followed by *en masse* post-fire seed release for both species (Sugnet, 1985; Vogl, 1973; Vogl et al., 1977). Historical fire frequency is poorly understood and likely varied substantially across the distributions of both species. Estimated mean fire return intervals for bishop pine range from 40 to 70 years in monodominant stands and 20–29 years in coast redwood (*Sequoia sempervirens*) stands where non-stand-replacing fire is typical (Finney and Martin, 1989; Sugnet, 1985). Fire histories overlapping the range of knobcone pine estimate mean fire return intervals from 30 to 90 years where closed-cone pine communities are interspersed with chapparal (van de Water and Safford, 2011) and 5–19 years where knobcone pine is a minor component in mixed-conifer stands characterized by non-stand-replacing fire and dominated by Douglas-fir or ponderosa pine (*Pinus ponderosa*) (Fry and Stephens, 2006; Taylor and Skinner, 1998). Population dynamics following a range of fire intervals suggest at least 30 years between stand-replacing fires are needed to support post-fire regeneration densities that develop into monodominant stands such as those in this study (Agne et al., 2022b). Therefore, we assume that 30 years represents the historical minimum interval between stand-replacing fires that support forests dominated by California closed-cone pines. Although there is evidence of higher frequency non-stand-replacing fire in both species ranges (Finney and Martin, 1989; Fry et al., 2012), this is typically associated with stands in which closed-cone pines are codominant with, or subordinate to, other conifer species, rather than the monodominant stands that are the focus of this study.

2.2. Study design and field sampling

To quantify fuel profile development over time, we established a chronosequence of plots representing 2–35 years TSF across the study area. To capture this range of TSF across California closed-cone pine forests, 15 fires (each representing a single TSF) were selected using Monitoring Trends in Burn Severity (MTBS) data (Eidenshink et al., 2007), species distribution maps, and local land management information to identify past fires since 1982 that were at least 100 ha in size and overlapped our target species' ranges (Appendix: Figure A1). Plot locations were at least 50 m from roads and covered the range of topographic positions and stand density within each fire perimeter. Each plot represented a single-aged cohort of closed-cone pine that established from a pulsed seed release following stand-replacing fire (defined as > 90% mortality of individuals from the previous pre-fire cohort). Plots were separated by a distance of at least 100 m, with shorter distances possible when plots were on opposing topographic positions (e.g., N vs. S aspect). The number of plots sampled varied between two and ten per fire due to sampling constraints (e.g., fire size, closed-cone pine forest area) with a total of 79 plots established in the summers of 2017 and 2018 (Table 1).

At each plot, we measured dead surface fuels (downed woody debris and litter depth), live surface fuels (standing live and dead herbaceous, shrub, and tree biomass < 2 m in height) and canopy fuels (live and standing dead tree and shrub biomass ≥ 2 m in height). Downed woody debris was measured along three transects (with the exception that 16 plots had two transects) established in randomly selected cardinal directions and using standard planar intercept methods (Brown, 1974). Total transect length varied between plots, as field plots from two separate studies were used; 4–6 m for 1-hr (<0.64 cm) fuels, 10–15 m for 10-hr (0.64–2.54 cm) fuels, 20–30 m for 100-hr (2.54–7.62 cm) fuels, and 35.6–54 m for 1000-hr (>7.62 cm) fuels (see Appendix A for detailed sampling methodology). We identified 1000-hour fuels to species when possible, categorized them using a 1–5 decay class rating system (Sollins, 1982), and measured the diameter of every piece where it crossed the transect. Litter depth was measured at one-meter intervals along two 18 m transects at each plot ($n = 36$) and estimated to the nearest 0.1 cm.

We measured live surface fuels along two 18 m transects at each plot using a point-intercept method (Fontaine et al., 2012; Tangney et al., 2022). We tallied individual interceptions of standing vegetation by our height pole at one-meter intervals along each transect ($n = 36$). For each vegetation interception, we assigned it to a height class (≤0.5 m, 0.5–1.0 m, 1.0–2.0 m) and live or dead status. We additionally classified the plant from which the interception was derived as live or dead, and identified it to species for trees and shrubs, or life form for forbs and graminoids (hereafter, combined as herbaceous). For all shrubs that were intercepted, total height and two perpendicular crown widths were

Table 1
Sample fires with number of plots per fire (n) and plot-level mean (standard deviation) post-fire California closed-cone pine stand characteristics.

Fire name	TSF[1] (years)	Fire year	Dominant species	n	Live BA[2] (m^2 ha^{-1})	Live density[3] (trees ha^{-1})	Average tree height (m)	QMD[4] (cm)
Cuesta	2	2015	PIAT[5]	7	NA	110,556 (63,088)	0.2 (0.1)	NA
Butler	5	2013	PIAT	2	1.06 (0.13)	7,043 (1,744)	0.6 (0.2)	1.4 (0.3)
North Ranch (Vegetation Management Unit)	5	2012	PIMU[6]	6	1.17 (1.00)	13,274 (10,001)	1.1 (0.4)	1.6 (1.0)
Stafford	6	2012	PIAT	2	0.53 (0.40)	1,837 (1,692)	1.8 (0.2)	2.0 (0.3)
North Ranch (North Unit)	7	2010	PIMU	5	5.62 (3.83)	45,910 (23,983)	1.1 (0.4)	1.2 (0.2)
North Ranch (South Unit)	8	2009	PIMU	4	3.91 (3.61)	6,381 (4,901)	2.2 (1.0)	3.2 (1.6)
Motion	10	2008	PIAT	8	5.30 (2.07)	3,493 (3,667)	4.2 (0.8)	5.6 (1.9)
Diablo	10	2007	PIMU	6	2.71 (1.79)	2,034 (1,319)	3.2 (1.3)	4.4 (1.9)
Bear	14	2004	PIAT	9	16.51 (6.25)	3,444 (4,898)	7.9 (1.7)	10.6 (4.2)
Whiskeytown	15	2003	PIAT	2	10.01 (3.14)	2,880 (1,804)	6.9 (0.4)	6.6 (0.7)
Sugar	19	1999	PIAT	6	19.70 (14.73)	4,689 (5,355)	7.5 (0.7)	8.7 (2.3)
Hwy 41	23	1994	PIAT	3	19.99 (12.50)	2,389 (1,641)	9.2 (2.3)	11.0 (2.5)
Vision	23	1995	PIMU	10	37.70 (17.06)	6,953 (9,156)	10.1 (2.6)	15.7 (8.4)
Las Pilitas	32	1985	PIAT	3	25.59 (3.40)	2,735 (448)	11.2 (0.5)	10.9 (1.6)
Diablo Canyon	35	1982	PIMU	6	14.33 (6.03)	710 (434)	13.3 (2.5)	16.2 (3.4)

[1] Time since fire at time of sampling, which occurred over two years, leading to fires that occurred in multiple years having the same time since fire.
[2] Basal area.
[3] A population estimate of total live tree density (distinct from the canopy fuel metric of live tree density estimated as trees $ha^{-1} \geq 2$ *m*).
[4] Quadratic mean diameter.
[5] Knobcone pine (*Pinus attenuata*).
[6] Bishop pine (*Pinus muricata*).

taken.

We measured canopy fuels and post-fire stand structure within a central subplot at each plot. Central subplot size radii varied with post-fire stand density and ranged from 2 to 18 m. If the central subplot radius was < 8 m, we estimated stand density within four additional 1 m radius microplots located in the cardinal directions from subplot center (total sampling area range: 25–1018 m^2). All trees were categorized as live or dead, assessed for structural damage (e.g., dead or broken top), and measured for diameter at breast height (DBH; 1.37 m above ground) and total height. We reconstructed stand structure conditions preceding the last stand-replacing fire by measuring the DBH of all standing and fallen snags. However, reconstruction was not possible at plots nine years TSF and older at which most snags had fallen (n = 56).

Ten of our 79 plots reburned in the 2018 Carr Fire; eight at 10 years TSF and two at 15 years TSF. The wildfire occurred approximately one month following initial fuels measurement, so that our fuels estimates approximate available fuel at the time of fire. We revisited these plots in May 2019, approximately 10 months following wildfire, to assess fire severity as determined by percent canopy tree mortality. We compared minimum and median fuel load values from plots where high-severity fire (>90% canopy tree mortality) occurred (n = 6) to understand how values for fuel loads across the chronosequence correspond to values capable of supporting high-severity fire.

2.3. Fuel calculations

2.3.1. Surface fuel load

We calculated the dead surface fuel load (Mg ha^{-1}) for each fuel size class (1-, 10-, 100-, 1000-hour) individually, using standard planar intercept methods with values for lodgepole pine as there are no published values for our focal species (Brown, 1974). We separated 1000-hour fuels further into sound (decay class 1–3; bole of downed log intact) and rotten (decay class 4–5; bole of downed log breaking apart). We averaged litter depth measurements for all transects within each plot (n = 36) to obtain plot-level litter depth estimates. Live surface fuels were calculated separately for each life form from point intercept data for each plot. The herbaceous fuel load (Mg ha^{-1}) was estimated by summing graminoid and forb biomass, which were each calculated from percent cover (estimated as the proportion of sample points at which a graminoid or forb was intercepted), using general graminoid and *Lupinus* spp. equations (Means et al. 1994). We estimated the live woody shrub fuel load (Mg ha^{-1}) using published equations employed by the Fuel Characteristic Classification System (Prichard et al. 2013) to estimate individual shrub crown biomass from shrub height and crown widths measured, summing across each plot and scaling to the hectare. The live woody tree fuel load (Mg ha^{-1}) was estimated by assigning each interception as foliage or branch and multiplying published values of specific leaf mass or oven dry weight (Abrams and Kubiske, 1990; Wilson et al., 1986), respectively, by the sampling area (defined as the intercept pole width * transect length), summing across each plot and scaling to the hectare (see Appendix: Table A1 for herbaceous and live woody fuel load equations). We quantified composition by allocating herbaceous, live woody tree, and live woody shrub fuel loads to three vertical strata (≤0.5, 0.5–1.0, 1.0–2.0 m), proportionally to the number of live and dead interceptions of each life form measured within each height class in the field. For shrubs that extended into the canopy layer, biomass was allocated to the surface and canopy layer proportionally to total height (see Appendix A for additional detail on herbaceous and live woody fuel calculations).

2.3.2. Canopy fuel load

Canopy fuels were estimated using field measurements and/or model equations. Stand height is the maximum live tree height at each plot, as measured in the field. For all stands with stand height > 2 m, canopy bulk density (kg m^{-3}) and canopy base height (m) were calculated from field measurements using equations developed for lodgepole pine (Cruz et al. 2003), as equations for knobcone pine and bishop pine are not available in the scientific literature. We calculated available canopy fuel load as total foliage biomass of all standing trees > 2 m plus 50% of live and dead branch biomass (Mg ha^{-1}) (Reinhardt et al., 2006). Foliage, live branch, and dead branch biomass were estimated using published equations for *Pinus* spp., or closely related species (Jenkins et al., 2003; Means et al., 1994; Prichard et al., 2013), summing across each plot and scaling to the hectare (see Appendix A for additional canopy fuel calculation detail). For stands with stand height < 2 m, we assumed canopy fuels were zero and that all trees were part of the live woody tree layer (described in surface fuel load calculations). We calculated the density of live trees in the canopy layer by summing the number of live trees > 2 m and scaling to the hectare (hereafter, live stand density [trees ha^{-1}]). Snag density (trees ha^{-1}) was calculated similarly and included all standing dead trees killed by the previous fire and standing dead trees > 2 m that had established post-fire and subsequently died. We calculated live and dead basal area (m^2 ha^{-1}) using the same subset of live and dead trees.

2.4. Legacy of vegetation structure preceding the most recent fire

We classified the pre-fire vegetation legacy of each plot (pre-fire forest or non-forest ecosystem) using field-based measurements of pre-fire structure and aerial imagery from the National Agriculture Imagery Program (NAIP) or National Aerial Photography Program (NAPP) (United States Department of Agriculture, 2020; United States Geological Survey, 2020). Where elements of the pre-fire stand (standing snags and dead shrubs killed by the last fire) were apparent, we used field measures. In plots ≥ 9 years TSF, most snags had fallen, and we relied on aerial imagery to reconstruct pre-fire vegetation legacy. We considered plots to be forested pre-fire if there were at least ten trees within 18 m of plot center prior to fire (~100 trees ha^{-1}). Plots classified as non-forested prior to the most recent fire generally had zero trees within 18 m of plot center prior to fire and were presumed forested via post-fire expansion from an adjacent forest ecosystem. Plots > 23 years TSF (n = 9) were not classified due to data availability limitations.

2.5. Statistical analysis

To address question 1 (fuel load development following fire), we used generalized additive models (GAMs) to assess the effect of TSF on all surface and canopy fuel variables. GAMs are highly flexible, are ideal for understanding nonlinear relationships (Simpson, 2018; Wood, 2006), and have been used in previous chronosequence studies of trends over TSF (Valentine et al. 2014, Jenkins et al. 2020). To assess the temporal trajectory of the surface fuel load, we fit models for six downed surface fuel response variables (1-hr, 10-hr, 100-hr, 1000-hr sound, and 1000-hr rotten fuel loads, litter depth), herbaceous, live woody shrub, and live woody tree fuel loads. Further, we used a descriptive approach to understand the composition of live surface fuels by plotting mean values within a single TSF for herbaceous, woody shrub, and woody tree biomass within three vertical strata (≤0.5, 0.5–1.0, 1.0–2.0 m) by live versus dead biomass. To assess canopy fuel loads, we fit models for eight canopy fuel response variables (canopy bulk density, available canopy fuel load, canopy base height, stand height, live stand density, snag density, live basal area, and dead basal area).

Each model fit to address question 1 included TSF as the predictor variable of interest and three biologically meaningful environmental covariates likely to affect stand growth and account for variation in productivity across the study area: 30-year mean annual standardized precipitation evapotranspiration index (SPEI), elevation, and heat load index (HLI). 30-year mean annual SPEI and elevation represent proxies for growing conditions expected to primarily vary between dominant species and regionally (i.e., among fire perimeters). 30-year mean annual SPEI (hereafter, mean annual SPEI) was represented using 800 m resolution gridded 30 year 1981–2010 normals obtained from the

Westwide Drought Tracker (Abatzoglou et al. 2017; https://wrcc.dri.edu/wwdt/). Elevation for each plot was obtained using a Garmin GPS unit. Topoclimatic differences within fire perimeters were represented by HLI, a measure that incorporates latitude, slope, and aspect into a single metric that corresponds to plot-level differences in solar radiation (McCune and Keon, 2002). Bishop pine and knobcone pine occupied distinct ranges of values for mean annual SPEI and elevation but are interspersed across HLI (Appendix: Figures A2–A7), suggesting these covariates capture distinctions between dominant species as well as variation within forests dominated by each species. Therefore, we did not include a separate term for species in the model as we expected the environmental covariates to adequately represent differences in environmental space occupied by the two species. Covariates were inspected for collinearity and concurvity prior to model implementation. To understand whether these covariates were useful additions to our models, for each response variable we fit a full model that included the focal predictor, TSF, and mean annual SPEI, elevation, and HLI as covariates, and a reduced model that included TSF as the sole predictor. We used a likelihood ratio test to compare the goodness of fit of the two models, and the full model form had a significantly improved fit over the reduced model for 15 of 17 variables (Appendix: Tables A2–A3). For consistency we chose to implement GAMs with the full model form for all response variables, but do not include exploration of covariate effects in the results as they are tangential to the research question (Appendix: Tables A4–A5).

To address question 2 (effect of pre-fire vegetation legacy on fuel profile trajectories), we fit additional GAMs for each fuel response variable assessed in question 1. Each model included the predictor variables of TSF, a categorical effect of pre-fire legacy (i.e., forest preceding the last fire vs. non-forest preceding the last fire), and a TSF-pre-fire legacy interaction term. The analysis included the subset of plots burned since 1994 ($n = 70$) for which there were pre-fire legacy classification data from either aerial imagery or field data.

For all models, we used restricted maximum likelihood estimation (REML) to choose smoothing parameters and the number of basis functions for each predictor variable (Wood, 2011). In general, this approach avoids overfitting, but we also visually inspected model fit for evidence of overfitting – instances in which REML resulted in knots (i.e., changes in the basis function) where there were no data for a given covariate. In these cases, we refit the model with successively fewer basis functions for that covariate until no knots occurred where data were lacking for any covariate in the model. After assessing model assumptions, all surface and canopy fuel variables were modeled using a scaled t-distribution for heavy tailed data. We performed all analyses in R version 3.6.0 (R Core Team, 2019). Modeled effect plots were produced with the packages "ggplot2" (Wickham, 2016), "ggpubr" (Kassambara, 2020), "viridis" (Garnier et al., 2018), and "voxel" (de la Garza et al., 2018). Likelihood ratio tests comparing candidate models were conducted with the package "lmtest" (Zeileis and Hothorn, 2002). Statistical analyses of continuous TSF effects on fuel loads using GAMs were conducted with the package "mgcv" (Wood, 2011; Wood et al., 2016). Given the variability inherent in fuels (Keane, 2016), we interpreted $P \leq 0.01$ as strong evidence of an effect, $P \leq 0.05$ as moderate evidence of an effect and $P \leq 0.10$ as suggestive evidence of an effect.

3. Results

3.1. Post-fire stand characteristics

All sampled stands were dominated by a single post-fire cohort of closed-cone pines, but stand structure differed greatly with TSF (Table 1). Mean density of the post-fire cohort (including trees in the surface and canopy layers) ranged from 110,600 (sd = 63,100) trees ha^{-1} at two years TSF to 710 (sd = 434) trees ha^{-1} at 35 years TSF. Mean live basal area in stands with trees above breast height ranged from 0.5 m^2 ha^{-1} at five years TSF to 37.7 m^2 ha^{-1} in stands at 23 years TSF. Quadratic mean diameter ranged from 1.1 cm at five years TSF to 16.1 cm at 35 years TSF, while mean tree height ranged from 0.2 m at two years TSF to 13.2 m at 35 years TSF. Stand characteristics were similar between the two species at comparable TSF (Table 1), supporting our approach of combining the species as a single forest type.

3.2. Surface fuel load

Dead surface fuels increased with TSF, but the magnitude of change differed among specific fuel components (Fig. 2, Appendix: Table A4). There was strong evidence of linear increases in 1-hr and 10-hr fuel loads over TSF (Fig. 2a, b), reaching estimated mean values of 0.6 Mg ha^{-1} and 4.0 Mg ha^{-1}, respectively, at 35 years TSF. There was suggestive evidence of an increase in the 100-hr fuel load until 15 years TSF, thereafter plateauing at an estimated mean value of approximately 7.0 Mg ha^{-1} (Fig. 2c). The 1000-h sound fuel load peaked at an estimated mean value of 13.7 Mg ha^{-1} at 11 years TSF, before declining to approximately zero by three decades post-fire (Fig. 2d). The 1000-h rotten fuel load increased linearly with TSF, but there was considerable variation around this relationship from 15 to 23 years TSF that was poorly captured by the model (deviance explained = 5.15, Fig. 2e). Litter depth increased with TSF, reaching an estimated mean value of 7.6 cm at 35 years TSF (Fig. 2f).

The live surface fuel layer was characterized by a rapid increase in biomass over the first 10 years TSF (Fig. 3a), although individual fuel components varied in their development (Fig. 2g–2i, Appendix: Table A4). Within the first 10 years TSF, live surface fuel biomass met or exceeded levels observed several decades post-fire (Fig. 3a). During this period, live surface fuels were composed mainly of live biomass from tree and shrub crowns, and to a lesser degree, herbaceous vegetation, mostly occurring below 1 m in height (Fig. 3b). As time progressed, dead biomass made up an increasing proportion of this fuel layer (Fig. 3a), and the proportion of biomass > 1 m in height increased over TSF (Fig. 3b). The herbaceous fuel load decreased over time, declining from 2.0 Mg ha^{-1} at two years TSF to approximately zero by 15 years TSF (Fig. 2g). Conversely, the live woody shrub fuel load increased linearly over TSF, reaching 8.9 Mg ha^{-1} on average at 35 years TSF (Fig. 2h). After 10 years TSF, live and dead shrub biomass made up the greatest proportion of live surface fuels (Fig. 3a). There was suggestive evidence that the live woody tree fuel load increased, peaking at 2.8 Mg ha^{-1} at 10 years TSF before declining to 0.5 Mg ha^{-1} at 35 years TSF (Fig. 2i). However, this model has relatively low explanatory power (relative deviance = 13.2, Appendix: Table A4) and does not capture the rapid increase and decline in the live woody tree fuel load between six and eight years TSF characterized by values two to five times the peak mean value (Fig. 3a).

3.3. Canopy fuel load

Canopy fuels generally increased over time since fire (Fig. 4; Appendix: Table A5). Available canopy fuel load increased up to a plateau of 13.5 Mg ha^{-1} by 23 years TSF (Fig. 4a). Canopy bulk density increased until its peak of 0.11 kg m^{-3} at 23 years TSF, decreasing to 0.05 kg m^{-3} after three decades post-fire (Fig. 4b). Canopy base height and stand height both increased over TSF (Fig. 4c, d). Live stand density of canopy trees peaked at 2,500 trees ha^{-1} at 19 years TSF, but individual plot densities varied by several orders of magnitude between eight and 23 years TSF (Fig. 4e). Live basal area increased with TSF, plateauing after 20 years TSF at approximately 19 m^2 ha^{-1} (Fig. 4g). Snag density did not vary with TSF (Fig. 4f), but dead basal area decreased from its peak at two years TSF to approximately zero by 10 years TSF before increasing again after 20 years TSF (Fig. 4h).

3.4. Pre-fire legacy effects on surface and canopy fuel loads

Pre-fire vegetation legacy had a strong effect on the trajectory of the

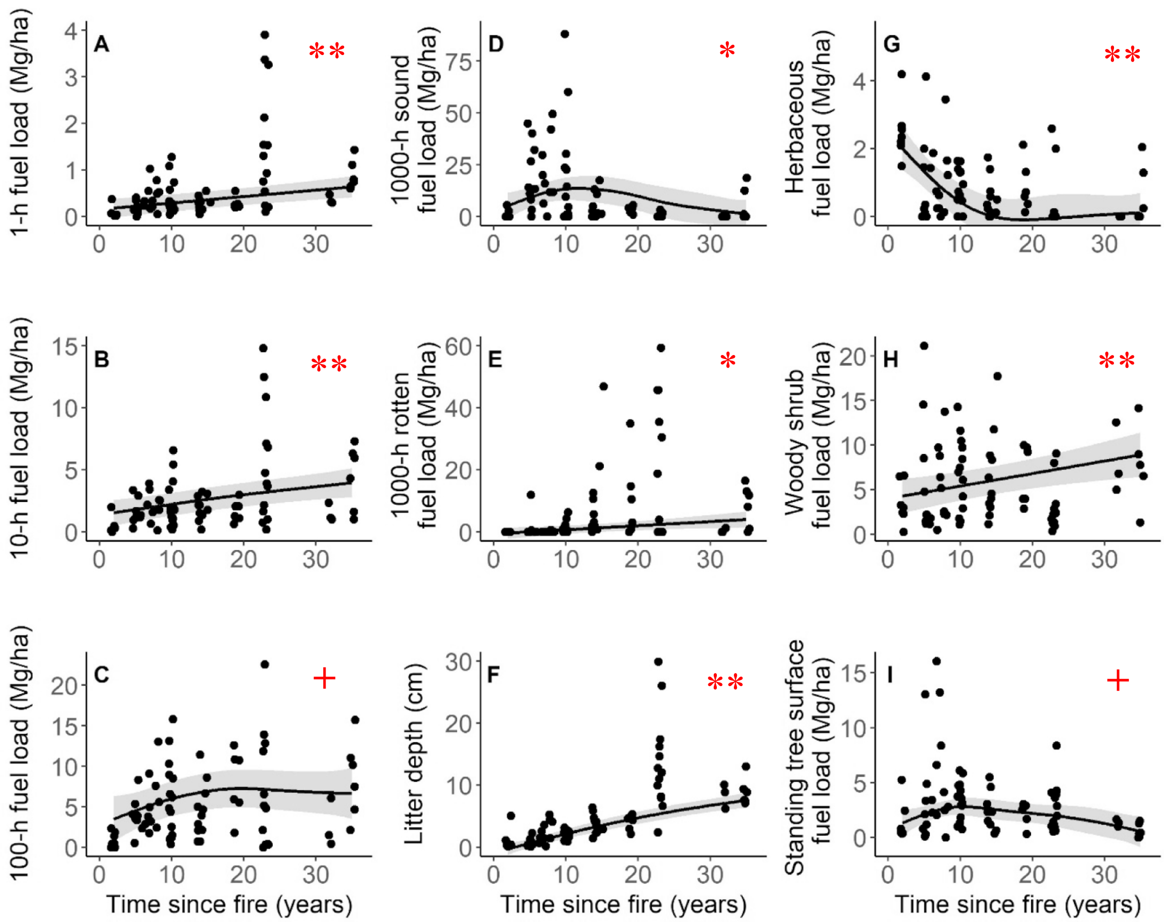

Fig. 2. Partial effects of time since fire (TSF) on surface fuel load variables from generalized additive models of the form ~ TSF + mean annual standardized evapotranspiration index (SPEI) + elevation + heat load index (HLI). Lines represent estimated partial effect, shading represents 95% confidence intervals, and each dot represents a plot (n = 79). Asterisks indicate strength of evidence of an effect of TSF according to $P < 0.01^{**}$ (strong), 0.05* (moderate), 0.1^{+} (suggestive).

dead surface fuel load and influenced live surface fuels to a lesser degree (Fig. 5). Downed woody debris of all size classes increased with TSF at pre-fire forested plots but remained stable at low levels across the chronosequence for pre-fire non-forested plots (Fig. 5a–e). Peak mean values for 1-hr, 10-hr, and 100-hr fuels were 2.6-, 2.8-, and 1.9-fold greater, respectively, at pre-fire forested versus pre-fire non-forested plots (Appendix: Table A6). At pre-fire forested plots, 1000-hr sound fuels increased to a mean of 18.0 Mg ha^{-1} at 9 years TSF before declining to approximately zero by 19 years TSF, while 1000-hr rotten fuels increased to a mean of 26.2 Mg ha^{-1} by 23 years TSF (Fig. 5d–e). Conversely, at pre-fire non-forested plots, there was no change in 1000-hr sound or 1000-hr rotten fuels, which remained under 5 Mg ha^{-1} from five years TSF onwards (Fig. 5d–e). The live woody shrub fuel load also followed separate early post-fire trajectories by pre-fire vegetation legacy, although trajectories converged by 10 years TSF (Fig. 5h). Litter depth, the herbaceous fuel load, and the live woody tree fuel load did not differ between plots that were forested versus non-forested pre-fire (Fig. 5f, g, i).

Canopy fuels varied minimally by pre-fire legacy; canopy bulk density, canopy base height, stand height, live stand density, and snag density were similar for plots that were forested and non-forested pre-fire (Fig. 6b–f). However, at approximately 19 years TSF available canopy fuel load and live basal area diverged by pre-fire legacy (Fig. 6a, g). Available canopy fuel load and live basal area at pre-fire non-forest plots were approximately 60% and 50%, respectively, of values for pre-fire forested plots at 23 years TSF (Appendix: Table A7). Further, dead basal area followed a U-shaped trend at pre-fire forested plots, reaching a minimum at 16 years TSF, but remained stable at a low level in pre-fire non-forested plots (Fig. 6h).

3.5. *Fuel profiles that supported stand-replacing fire shortly after data collection*

For plots that burned in the 2018 Carr Fire shortly after fuels data were collected, median values for pre-fire fuel loads were, in general, greater in plots that burned with stand-replacing fire than in those that burned with non-stand-replacing fire, although the range of values overlapped for most fuel components (Table 2). Fuel loads comparable to those that supported stand-replacing fire in the 2018 Carr Fire were commonly apparent in stands by 10–15 years since the previous fire. Downed surface fuel loads that supported stand-replacing fire in the 2018 Carr Fire were generally present by 10 years TSF, whereas canopy fuel loads that supported stand-replacing fire were present 9–15 years TSF across plots (Table 2). Woody shrub fuel loads that supported stand-replacing fire in the Carr Fire were often reached by as early as two years TSF across plots (Table 2), though the range of woody shrub fuel loads that supported stand-replacing fire covered the range seen across the fuels chronosequence (Table 2).

4. Discussion

Understanding when and where changing disturbance regimes may result in linked disturbances that erode forest resilience is critical for managing forests under increasingly fire-prone climate conditions. Our

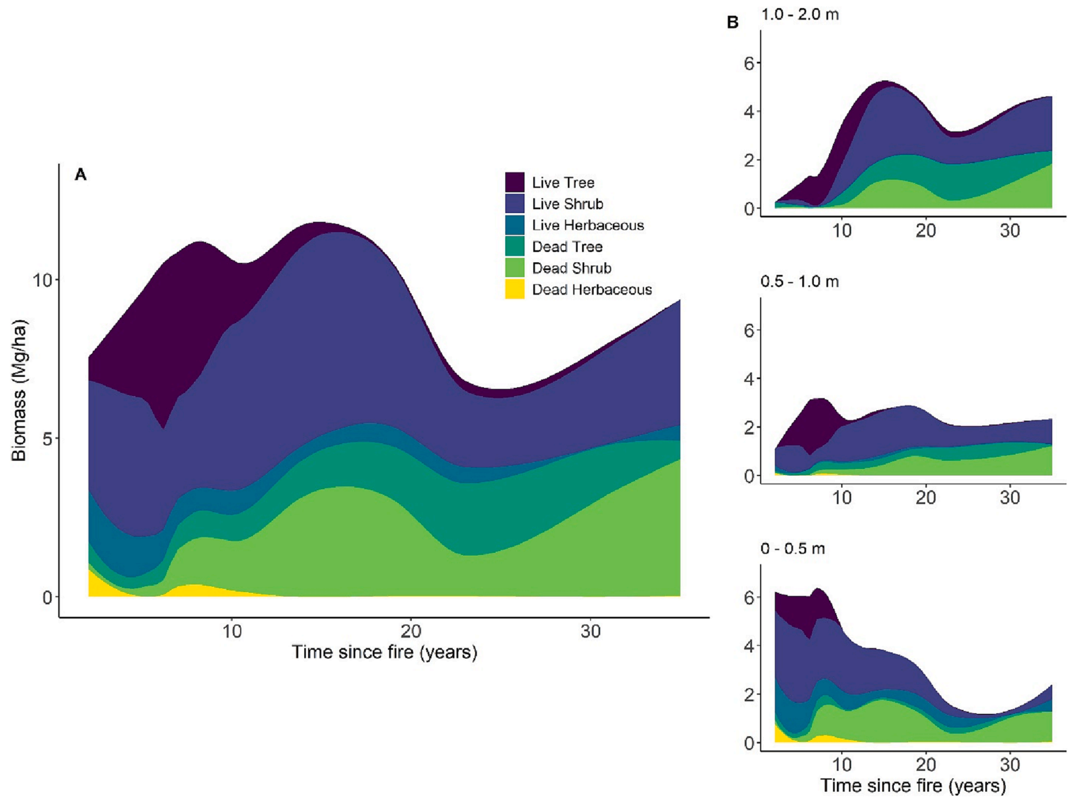

Fig. 3. A: cumulative standing biomass in the surface layer (within 0–2 m of the ground) b: Cumulative standing biomass in the surface layer by vertical stratum (1.0–2.0, 0.5–1.0, and 0–0.5 m of the ground). Colors represent averages of plot-level estimates of each biomass category for each measured time since fire (TSF) interpolated across the chronosequence using a loess smoother (span = 0.5).

findings demonstrate that fuel accumulation in California closed-cone pine forests occurs rapidly following stand-replacing fire and are comparable to those that can support severe reburns within ten years. The period of fuel limitation is brief compared with historical minimum interval between stand-replacing fires that supported high levels of post-fire regeneration, suggesting increased short-interval severe reburns can occur with climate warming. Pre-fire vegetation legacy was a strong driver of fuel profile trajectories; stands that were non-forest pre-fire (comprising approximately 25% of sampled plots) were characterized by an extended period of comparatively low dead surface fuel loads and therefore lower capacity to carry severe fire as compared to areas that were forested pre-fire. Timing of fuel development and pre-fire vegetation legacy can have substantial effects on subsequent fire activity and stand-scale forest resilience with important implications for timing and effectiveness of management interventions (Prichard et al., 2017).

4.1. Rapid accumulation of surface and canopy fuels

Our finding that fuels met or exceeded values that supported a severe reburn by approximately 10 years post-fire provides insight into the key mechanism behind reburn patterns observed in coniferous forests in the western US (Buma et al., 2020; Harvey et al., 2016; Parks et al., 2015). Fuel accumulation followed a similar pattern to those described in previous studies of post-fire fuel dynamics, but on a trajectory aligned with accelerated stand dynamics. Dead surface fuel loads peaked or plateaued, coinciding with the processes of snag fragmentation and snagfall (Dunn and Bailey, 2015; Hall et al., 2006; Harmon et al., 1986) while live surface fuel loads accumulated rapidly due to prevalence of shrub species with fire-adapted traits that facilitate early and sustained post-fire growth (Fontaine et al., 2012). Canopy fuel loads peaked during the canopy closure phase, as is typical in other coniferous forests (Agee and Huff, 1987), remaining high across the chronosequence. Each of these fuel layers can be critical for driving severe reburns, as young California closed-cone pine forests are composed of trees with relatively thin bark and thus can experience stand-replacing fire as either severe surface or crown fire (Keeley and Zedler, 1998).

Dead surface fuel loads began to accumulate rapidly following fire, driven by near total transition of the pre-fire cohort from standing dead to surface fuel by 10 years TSF. While fine woody surface fuel loads within the first two decades post-fire were similar to peak values at similar TSF in mixed conifer and ponderosa pine forests (Dunn and Bailey, 2015; Hall et al., 2006), accumulation continued in California closed-cone pine forests until at least 35 years TSF. Inputs are predominantly driven by fragmentation of snags and fire-killed shrubs prior to post-fire snagfall, while inputs after snagfall can be attributed to density-dependent mortality of overstory trees (Keyser et al., 2009). Dense post-fire tree establishment immediately following fire in serotinous forests leads to earlier canopy closure than documented in non-serotinous forests (Harvey et al., 2011), while associated early crown recession provides a consistent input of fine fuels following snagfall that is absent from non-serotinous forests that establish and develop over a longer period following fire (Stevens-Rumann et al., 2020). Conversely, coarse woody surface fuels peaked at 11 years TSF, at least 10 years earlier and at 10–30% of peak fuel loads observed in other coniferous forests (Dunn and Bailey, 2015; Hall et al., 2006; Stevens-Rumann et al., 2020). Although many coniferous forests have high snag fall rates in the first decade post-fire, snag retention for decades is common (Everett et al., 1999), compared with our findings of near zero standing dead basal area by 10 years TSF (Fig. 4h), driving the early peak in the coarse woody surface fuel load. The rapid snag fall rate in California closed-cone pine forests is related to relatively small tree size (Grayson et al., 2019) and strong winds driving early snagfall along the coast (S. Bisbing, personal observation). Small tree size and low stand basal area compared to other coniferous forests (Vogl et al., 1977) translates to relatively low peak

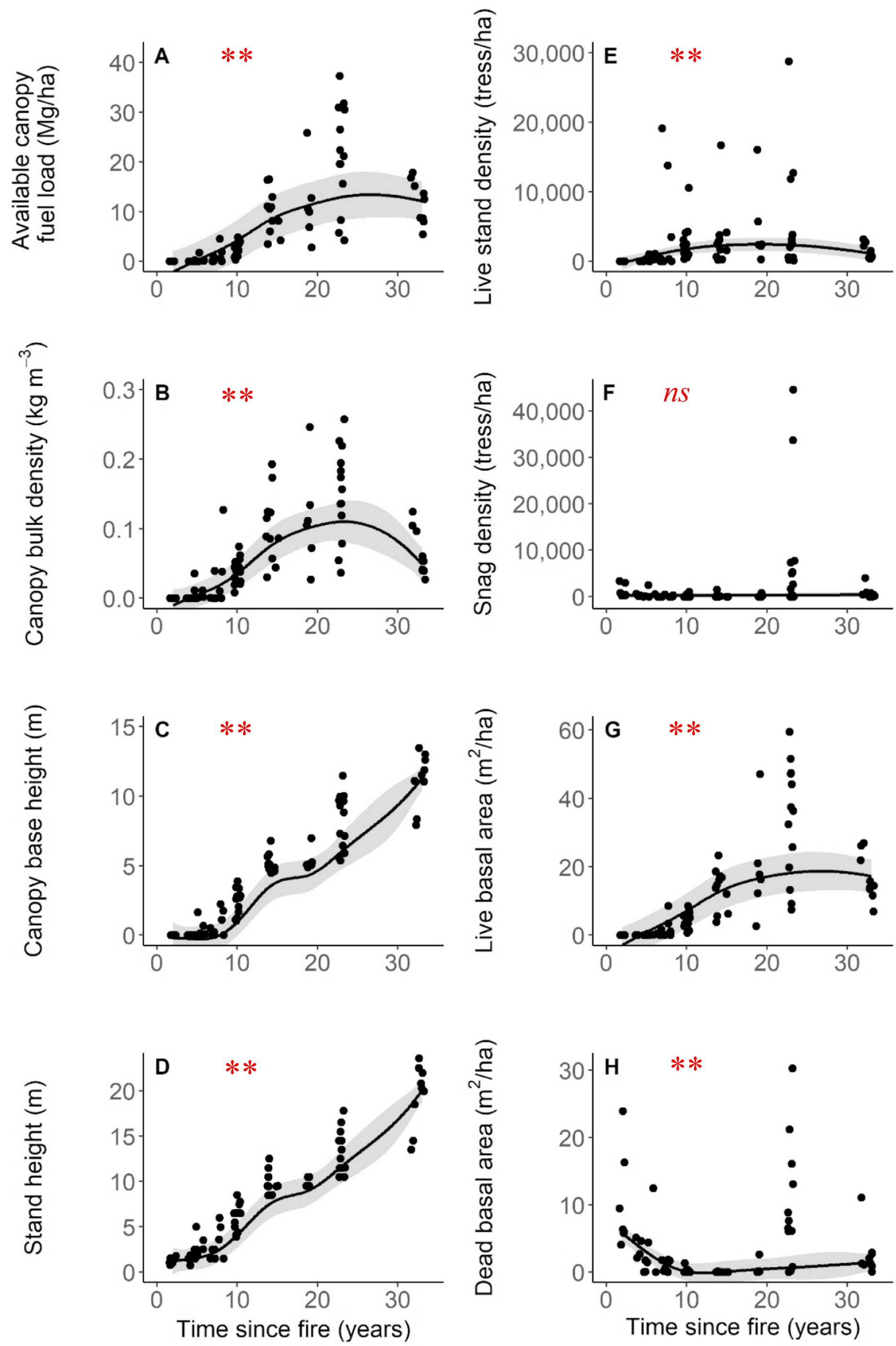

Fig. 4. Partial effects of time since fire (TSF) on canopy fuel variables from generalized additive models of the form ~ TSF + mean annual standardized evapotranspiration index (SPEI) + elevation + heat load index (HLI). Lines represent estimated partial effect, shading represents 95% confidence intervals, and each dot represents a plot (n = 79). Asterisks indicate strength of evidence of an effect of TSF according to $P < 0.01^{**}$ (strong), 0.05^{*} (moderate), 0.1^{+} (suggestive).

coarse woody surface fuel loads, although structurally similar jack pine and Baker cypress forests have coarse woody surface fuel loads comparable to those observed in this study at similar TSF (McNamara et al., 2019b; Stocks, 1987). While coarse woody surface fuels were generally under the threshold of fuel loads associated with severe surface fire (Sikkink and Keane, 2012), evidence from plots that burned in the Carr Fire (Table 2) shows that stand-replacing fire can occur in the absence of substantial downed coarse wood (<5 Mg ha^{-1}) in young closed-cone pine forests.

Rapid and sustained live surface fuel accumulation from post-fire shrub growth differs from other serotinous forests in colder climates (e.g., lodgepole pine forests) but may be an important characteristic of serotinous forests in warmer Mediterranean regions, such as California. By two years post-fire, the mean woody shrub fuel load reached values comparable to those that burned with stand-replacement in the Carr Fire (Table 2), exceeding that of both young and mature lodgepole pine forests by ~ 2–40x (Morris et al., 2023; Nelson et al., 2016) but was comparable to values reported for mature Baker cypress forests in California at similar TSF (McNamara et al., 2019b). Species with adaptations such as resprouting and soil stored seed banks that facilitate rapid

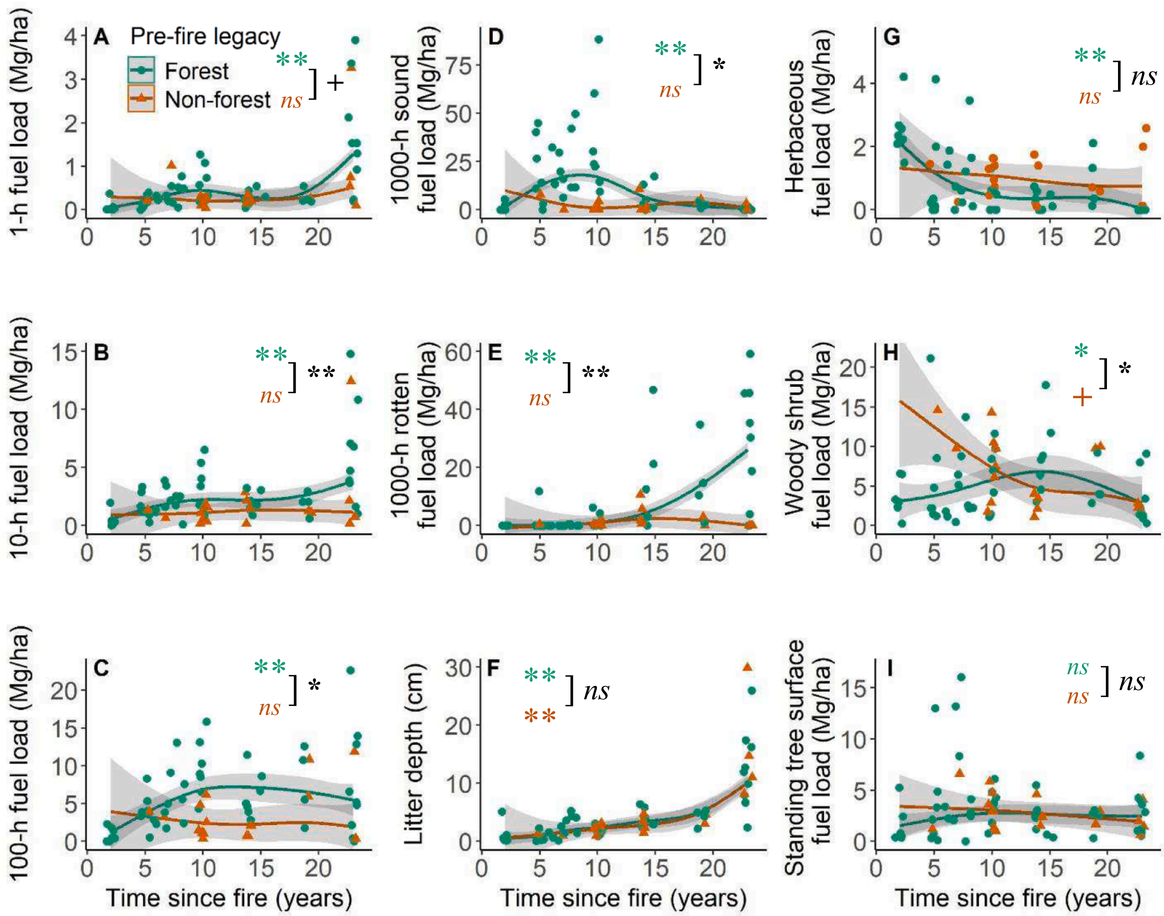

Fig. 5. Effects of time since fire (TSF) on surface fuel load variables from generalized additive models of the form ~ TSF + pre-fire vegetation legacy + TSF * pre-fire vegetation legacy, for 2–23 years TSF. Lines represent the estimated effect of TSF for each pre-fire vegetation legacy, shading represents 95% confidence intervals, and each dot represents a plot (n = 70). Asterisks indicate strength of evidence of an effect of pre-fire vegetation legacy (outside the bracket) and TSF * pre-fire vegetation legacy (within the bracket) according to $P < 0.01^{**}$ (strong), 0.05* (moderate), 0.1^{+} (suggestive).

post-fire growth (Fontaine et al., 2012) were common in the study area and likely drive this pattern. Early post-fire development of live surface fuels can drive short-interval severe reburns in forests characterized by stand-replacing fire (Agee and Huff, 1987; Harvey et al., 2016), particularly where severe surface fire can be stand-replacing, as is the case for young closed-cone pine stands (Vogl et al., 1977). The woody shrub fuel load continued to increase over time rather than plateauing after the canopy closure phase as in some conifer forests (Dunn and Bailey, 2015). This suggests that fuels can support severe surface fire for at least 35 years, although potential for severe surface fire may decrease at longer time scales (McNamara et al., 2019b; Odion et al., 2010). Further, the live surface layer increased with respect to proportion dead from 10 to 20 years TSF, similar to trends in mixed chaparral (Bohlman et al., 2018). Dead material accumulates under live shrub crowns due to competition and shading (Regelbrugge and Conard, 2002) and is associated with increased surface heating and fire duration (Fontaine et al., 2012). Live and dead shrub material also became evenly distributed across the vertical profile of the surface layer by 20 years TSF, increasing the potential for crown fire initiation given a surface fire, especially where canopy base heights are low (Van Wagner 1977).

Rapid canopy fuel development well before the historical minimum interval between stand-replacing fires suggests the potential for short-interval crown fire occurrence. Canopy fuels increased through the canopy closure phase, before stabilizing at a level above that required to support high-severity fire, similar to trends in other forests characterized by stand-replacing fire regimes (Agee and Huff, 1987; Nelson et al., 2017). The mean available canopy fuel load stabilized by 20 years TSF at 13.5 Mg ha^{-1}, comparable to values observed at similar TSF in serotinous jack pine and Aleppo pine (*P. halepensis*) forests and approximately 50% greater than those in young lodgepole pine forests (Mitsopoulos and Dimitrakopoulos, 2007; Nelson et al., 2016; Stocks, 1987). Conversely, mean canopy bulk density, which peaked at 0.11 kg m^{-3} around 25 years TSF, was low at 50–75% of values from other serotinous forests of similar TSF (Mitsopoulos and Dimitrakopoulos, 2007; Nelson et al., 2016). Despite relatively low canopy bulk density values, by 15 years TSF, mean canopy fuel values exceeded those modeled to carry active crown fire in mature Spanish pine forests under moderate burning conditions (Fernández-Alonso et al., 2013) and supported stand-replacing fire in the Carr Fire (Table 2). However, plots that experienced non-stand-replacing fire had distributions that overlapped most fuel profile components (Table 2), suggesting that fire weather and other stochastic factors also had a strong effect on fire severity. Although canopy bulk density values exceeding 0.1 kg m^{-3} are more likely to support active crown fire under a range of weather conditions (Agee, 1993), extreme fire weather is common across the range of California closed-cone pines (Son et al., 2021). Therefore, while active crown fire potential in California closed-cone pine forests is highest between 19 and 25 years TSF, canopy fuels are generally sufficient to carry crown fire by 15 years TSF, and earlier where burning conditions are extreme. Furthermore, as extreme fire conditions become more common with continued climate warming (Williams et al., 2019), fuel thresholds for active crown fire are likely to further decrease.

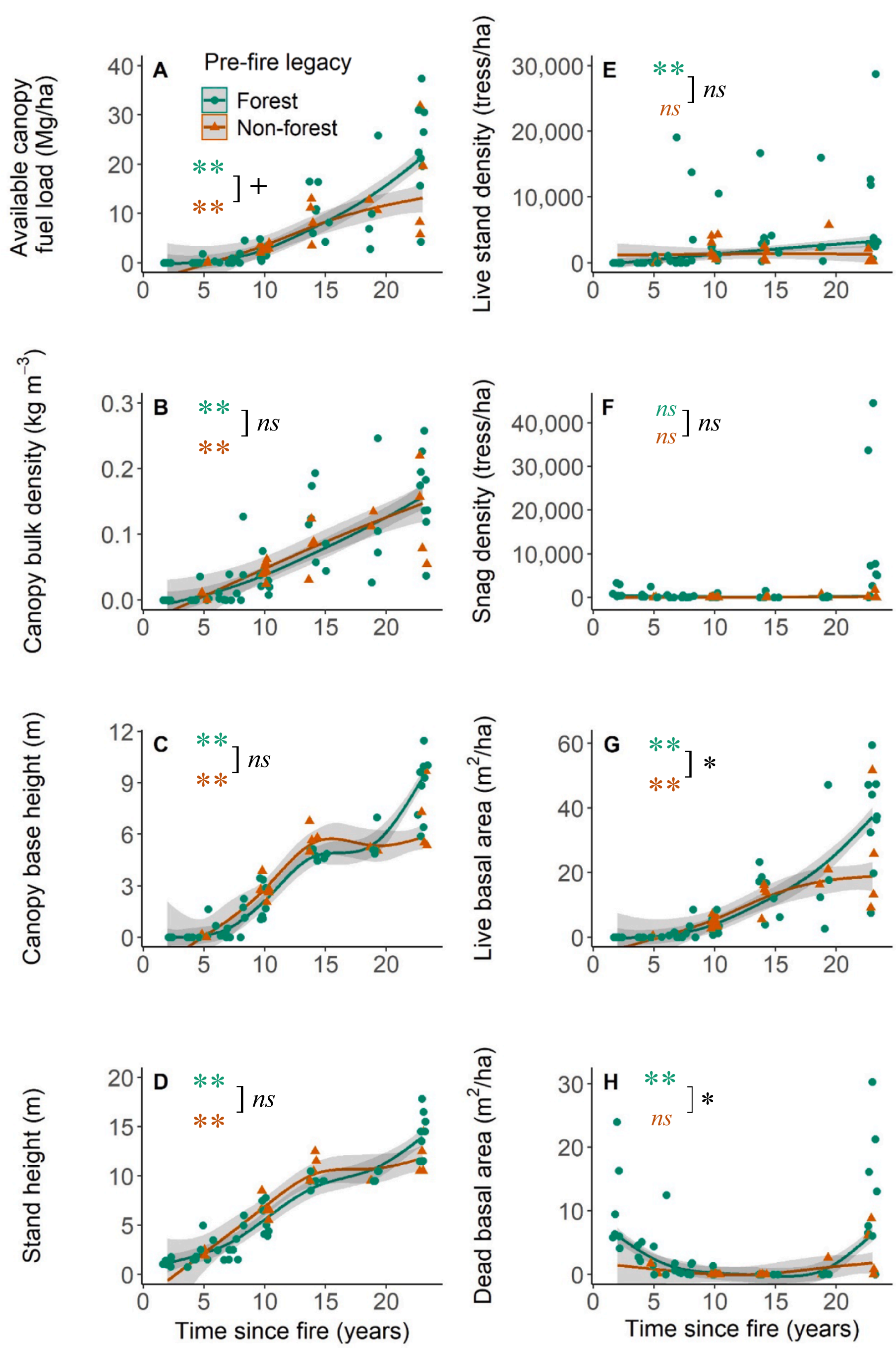

Fig. 6. Effects of time since fire (TSF) on canopy fuel variables from generalized additive models of the form ~ TSF + pre-fire vegetation legacy + TSF * pre-fire vegetation legacy, for 2–23 years TSF. Lines represent the estimated effect of TSF for each pre-fire vegetation legacy, shading represents 95% confidence intervals, and each dot represents a plot (n = 70). Asterisks indicate strength of evidence of an effect of pre-fire vegetation legacy (outside the bracket) and TSF * pre-fire vegetation legacy (within the bracket) according to $P < 0.01^{**}$ (strong), 0.05* (moderate), 0.1^{+} (suggestive).

4.2. *Fuel profile trajectories differ by pre-fire vegetation legacy*

The contrast between fuel profile trajectories in forests with differing pre-fire vegetation legacies has important implications for the likelihood of severe reburn, given a subsequent fire. Nearly 25% of sampled plots were non-forest prior to the most recent fire, showing that post-fire expansion of closed-cone pine forests can occur through nearby seed dispersal (Forrestel et al., 2011), or an *in situ* seed source, as is more common for many serotinous species (He et al., 2004; McNamara et al., 2019a). At plots that were non-forest prior to the most recent fire, dead surface fuel loads remained low for over two decades for all fuel sizes, reflecting values comparable to those in oak woodlands with a low-intensity surface fire regime (Tietje et al., 2002). These values are a fraction of that in forest-dominated ecosystems at similar TSF (Braziunas et al., 2023; Dunn and Bailey, 2015; Nelson et al., 2016; Stevens-Rumann et al., 2020). Conversely, minor differences in live surface and canopy fuels by pre-fire vegetation legacy indicate similar reproductive capacity of shrub or tree species within dispersal distance (Turner et al., 2019), although this trend may differ following short-interval severe reburns due to decreased seed dispersal from young forests (Gill et al., 2021; Harvey et al., 2023). Divergence in the canopy fuel profile between 19 and 23 years TSF suggests that differences in post-fire forest structure become more apparent following the canopy closure phase, but stands established from both pre-fire vegetation legacies have canopy fuel loads comparable to those sufficient to carry crown fire in many forests (Fernández-Alonso et al., 2013; Mitsopoulos and Dimitrakopoulos, 2007; Roccaforte et al., 2008). Therefore, susceptibility to severe surface fire may be delayed in pre-fire non-forested

Table 2
Medians (range) of pre-fire fuel profile values from plots that burned with stand-replacing fire (>90% canopy mortality, n = 6) and non-stand-replacing fire (<90% canopy mortality, n = 4) in the 2018 Carr Fire.

Fuel variable	Stand-replacing	Non-stand-replacing
1-hr fuel load (Mg ha^{-1})	0.22 (0.09 – 0.55)	0.20 (0.04 – 0.32)
10-hr fuel load (Mg ha^{-1})	1.69 (0.93 – 3.08)	0.45 (0.19 – 1.26)
100-hr fuel load (Mg ha^{-1})	5.74 (1.16 – 8.60)	1.26 (0.37 – 6.19)
1000-hr sound fuel load (Mg ha^{-1})	1.27 (0 – 22.60)	0.46 (0 – 4.58)
1000-hr rotten fuel load (Mg ha^{-1})	3.27 (0.63 – 46.89)	0 (0 – 0)
Litter depth (cm)	2.6 (1.8 – 3.0)	2.1 (1.0 – 3.2)
Herbaceous fuel load (Mg ha^{-1})	0.77 (0.12 – 1.40)	1.18 (0.47 – 1.64)
Live woody shrub fuel load (Mg ha^{-1})	8.63 (2.90 – 17.77)	8.30 (1.76 – 14.30)
Live woody tree fuel load (Mg ha^{-1})	3.26 (0.38 – 4.75)	2.18 (1.03 – 5.85)
Available canopy fuel load (Mg ha^{-1})	4.12 (2.73 – 8.18)	2.73 (2.06 – 3.66)
Canopy bulk density (kg m^{-3})	0.057 (0.042 – 0.086)	0.042 (0.024 – 0.056)
Canopy base height (m)	2.9 (2.1 – 4.9)	2.8 (2.6 – 3.9)
Stand height (m)	6.5 (5.5 – 9.5)	6.5 (6.5 – 8.5)
Live stand density (trees ha^{-1})	2,323 (906 – 10,568)	2,533 (535 – 4,287)
Snag density (trees ha^{-1})	0 (0 – 127)	0 (0 – 0)
Live basal area (m^2 ha^{-1})	6.77 (3.68 – 12.09)	4.28 (2.62 – 6.59)
Dead basal area (m^2 ha^{-1})	0 (0 – 0.17)	0 (0 – 0)

compared with pre-fire forested stands due to low dead surface fuel loads, but overall fuel limitation declines after 15 years TSF due to growing canopy fuel loads that can support severe fire in stands with both pre-fire vegetation legacies. Additional pre-fire stand characteristics not investigated here — such as stand age, size class distribution, stand development pathway, stand-level variation in serotiny and canopy seed bank size — may contribute to additional variation in fuel profiles not explained by our models, and could be investigated in future studies of fuel dynamics over time.

Pre-fire vegetation legacy of non-forest may serve as a useful analog to understand how fuel profiles could influence subsequent fire activity following future short-interval severe reburns. Compared to longer intervals, short-interval severe reburns can drastically reduce downed woody surface fuels (Donato et al., 2016; Stevens-Rumann et al., 2020), similar to the difference we observed between pre-fire non-forest and pre-fire forest stands. Delayed development of the dead surface fuel load combined with comparable stand development suggests that stands resulting from forest expansion following fire or repeat severe fires could serve as unburned or low-severity patches in subsequent fires. Such areas could provide a seed source for regeneration of adjacent stands that would otherwise experience immaturity risk (Gill et al., 2021) and/or type conversion to non-forest.

4.3. Managing for resilience in closed-cone pine forests

Rapid fuel recovery in California closed-cone pine forests suggests that managers can expect young forests could experience severe reburn well before the historical minimum interval between stand-replacing fires that once supported high levels of regeneration. Fuels were historically not limiting to fire activity in closed-cone pine forests. However, warming climate and increased anthropogenic ignitions (Balch et al., 2017; Westerling et al., 2011), coupled with our findings, suggest that these forests could experience stand-replacing fire at least three times sooner post-fire than the estimated historical minimum interval between stand-replacing fires of 30 years (Agne et al., 2022b; Sugnet, 1985; van de Water and Safford, 2011). Short-interval severe reburns remain relatively rare across the study area (Reilly et al., 2019), but where fire occurs prior to accumulation of a sufficient canopy seed bank, their occurrence could result in the erosion of stand-scale resilience through compound effects on the demography and structure of serotinous forest stands (Brown and Johnstone, 2012; Keeley et al., 1999). Cone production begins in closed-cone pine trees between four and six years of age (Agne et al., 2022a; Bisbing et al., 2023), but sufficient canopy seed bank storage for stand replacement does not occur until ~15 years TSF (Agne et al., 2022b). Therefore, closed-cone pine stands are likely to be resilient to severe reburn except from ~10–15 years TSF, where fuels can support severe reburn, but the canopy seed bank is relatively small. Where conserving serotinous populations is a priority, suppressing fire within these stands may be warranted. However, this period coincides with snagfall and accumulation of 1000-hr fuels, along with increased woody shrub biomass capable of supporting higher intensity fires (Weatherspoon and Skinner, 1995), posing danger to firefighters and challenges to fireline construction (Page et al., 2013). Conversely, where reduced serotinous populations are desired, occurrence of short-interval severe reburns may reduce density (Agne et al., 2022b), but how such fire activity affects the vegetation community is uncertain. Relatively short fire intervals may favor serotinous conifer expansion where they occur in mixed conifer stands (Buma et al., 2013; Reilly et al., 2019), while non-native grass cover may increase where severe reburns occur rapidly enough to decrease serotinous populations (Smith et al., 2019).

Fuel reduction treatments are often considered in fire-prone forests as a tool to protect structures and valued resources, particularly in the wildland-urban interface. However, such treatments are costly, and optimizing treatments to mitigate potential for severe fire is often desired. Our findings suggest that fuel reduction treatments would need to be carried out on a < 10-year interval to meaningfully reduce potential for severe fire, and rapid recovery of live surface fuels may further curtail the longevity of treatments. Feasibility of such frequent treatments may be limited to small spatial extents (Agee and Skinner, 2005), suggesting that treatments should be prioritized to protect areas of high ecological, social, or cultural value. Trade-offs of fuel reduction treatments with competing objectives such as plant population conservation represent management challenges (Safford et al., 2018) differing by the mechanism of fuel reduction; mechanical treatments may deplete seed sources for obligate seeding plant species, while there are considerable difficulties with implementation of prescribed burning in closed-cone pine forests (Fry et al., 2012). Further, both treatment types may be entirely unfeasible in high density stands of small trees, as is common for this forest type for several decades following establishment (Agne et al., 2022a). However, dead surface fuel loads are low for decades after fire in areas of post-fire forest expansion into non-forest. Such areas are often localized, existing in a mosaic of forest and non-forest patches (Forrestel et al., 2011), and the resultant post-fire heterogeneity could create patches with lower resistance to control or greater tree survival in a subsequent fire (Sikkink and Keane, 2012). Therefore, divergent outcomes between stands could result in increased resilience of closed-cone pine forests to short-interval severe reburns across a broad landscape by retaining a seed source to regenerate adjacent stands. Stands with a pre-fire vegetation legacy of non-forest could also be identified as natural fire breaks or areas where surface fire intensity may be lower in a subsequent fire, particularly within ~15 years TSF prior to substantial canopy fuel load development.

5. Conclusions

Rapid post-fire accumulation of fuels suggests that closed-cone pine forests may be vulnerable to short-interval severe reburns at frequencies far exceeding the historical minimum interval between stand-replacing fires as the climate continues to warm. Pre-fire vegetation legacy strongly influences fuel profiles, and a mosaic of pre-fire vegetation may promote resilience to short-interval severe reburns at broad spatial scales. Understanding how trajectories of fuel accumulation align with development of the canopy seed bank is important for understanding the potential for serotinous forest resilience to increasing frequency of short-interval severe reburns.

CRediT authorship contribution statement

Michelle C. Agne: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration. **Joseph B. Fontaine:** Conceptualization, Methodology, Investigation, Writing – review & editing, Funding acquisition. **Neal J. Enright:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition. **Sarah M. Bisbing:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Brian J. Harvey:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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